

Aspects of the population ecology of the Green and golden bell frog *Litoria aurea* at the northern end of its range

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ABSTRACT

Development of appropriate conservation programs for threatened species requires a basic understanding of their population ecology. We studied a population of the Green and golden bell frog *Litoria aurea* in the far north of its range. This population occupies a coastal lagoon within Yuraygir National Park. Permanent tagging of frogs was conducted between August 1998 and March 2003. Population estimation based on the mark and recapture of frogs in 1998-99 suggested that the population contained at least 100 adult male frogs. Approximately 75 male bell frogs called from around the lagoon on one night in November 2001. The number of females captured in any year was low and it is unclear whether this is due to low detectability associated with irregular use of breeding sites or a highly skewed sex ratio. More than 60% of tagged male frogs were recaptured across one active season, but only two were recaptured outside the season of initial capture. This suggests that few male frogs live longer than about 2 years as adults. Breeding was erratic over a 6-year period and only one major metamorphosis event was observed. It appears that bell frogs may have greater breeding success in ephemeral ponds forming away from the lagoon, though there is a risk that these ponds may not persist for tadpoles to complete development. Frogs in this northern population were predominantly brown in colour, suggesting some morphological and genetic differentiation from southern populations in which most frogs are predominantly green. Further study of this important population is needed to more adequately determine the size of the female component of the population, and to better understand the limits on successful breeding. These issues will influence our understanding of the viability of the population, and therefore our ability to devise appropriate management actions. This study provides the first published account of aspects of the population ecology of the Green and golden bell frog in relatively undisturbed natural habitat.

Key words: bell frog, *Litoria aurea*, endangered frog, population monitoring

Introduction

The conservation and management of threatened species is dependent on an adequate understanding of their population ecology. Without this information uncertainty will arise over management actions that are needed to secure the viability of populations. For example, whether populations are sufficiently large to cope with short-term environmental variation, or whether populations are so diminished that removal to a captive environment is required.

For widespread threatened species, an important priority is to conserve populations throughout their geographic range (e.g. Murphy and Noon 1992; Goldingay 1996). This will ensure the conservation of genetic diversity and local adaptation, but also guard against all populations being exposed to extreme environmental conditions simultaneously (Goldingay and Lewis 1999). There is also a valid argument for paying management attention to populations at the edge of a species' range because these may be genetically and morphologically distinct (Lesica and Allendorf 1995; Lewis and Goldingay 1999).

There are few published studies on the population ecology of Australian frogs, although several studies have been published in recent years (e.g. Richards *et al.* 1993; White 1993; Gillespie and Hollis 1996; Williamson and Bull 1996; Goldingay and Lewis 1999; Goldingay *et al.* 1999; Pyke and White 1999). Some of these have

involved census procedures that provide only an index of population size (e.g. counts of calling males). While useful and necessary when attempting to monitor large numbers of populations, there is a need for more detailed assessment of population parameters.

The green and golden bell frog *Litoria aurea* is listed as a threatened species in New South Wales (NSW) and by the Australian Commonwealth. Due to its former abundance around Sydney and its presence at the Sydney Olympics site, it has achieved a high level of recognition in the Australian community (Pyke and White 2001; Christy 2003). These features have prompted many studies of its ecology (see Pyke and White 2001). However, there are few published accounts of its population ecology. This is likely to limit attempts to conserve this species.

The green and golden bell frog was found historically from near Byron Bay in north-east NSW, south to East Gippsland, and west to Bathurst and Tumut (White and Pyke 1996). The most northern populations currently known occur in Yuraygir National Park, some 90 km south of the former northern extremity (Lewis and Goldingay 1999). This area also represents one of the few where the green and golden bell frog occupies natural habitat (White and Pyke 1996). Thus, populations in this National Park are viewed as highly significant to the conservation of the species. Currently,

there is no published account of the population ecology of this species in natural coastal habitat. cursory censuses of the population in Yuraygir National Park suggest that only a small number of frogs may be present (Clancy 1996; Lewis and Goldingay 1999). The primary aim of this study was to describe aspects of the population ecology of the green and golden bell frog in Yuraygir National Park, including a more detailed assessment of the size of the population.

Methods

Study area

Yuraygir National Park is a large protected area located to the east of Grafton in north-east NSW (Fig. 1). There are two main areas where bell frogs have been located. One is near Diggers Camp, about 4 km north of Woolli. The other is at Station Creek (Ck), about 15 km south of Diggers Camp. Few frogs (<15) have been detected previously at either site (see Lewis and Goldingay 1999). This study focussed on Station Ck because frogs were more reliably detected there. The large distance between sites by road (ca. 60 km) precluded conducting detailed surveys concurrently at both sites.

Bell frogs at Station Ck occur at three locations (Clancy 1996; Lewis and Goldingay 1999): near the Station Ck rest area, in a dam along Station Ck Road and at Blue Lake and its immediate surrounds (Fig. 1). The lake is a large coastal lagoon measuring ca. 50-150 m x 800 m. These three locations are sufficiently close to each other (within 0.5-1 km) that it is likely that frogs migrate among sites. Two bell frogs were detected in the dam in 1997, but this site was later dropped from regular surveys after we failed to detect frogs on several occasions. Two large ephemeral ponds regularly form approximately 200 m east of the Station Ck rest area. These areas and a section of the small tributary of Station Ck near a footbridge, were surveyed during each visit. Most survey effort was focussed on the southern end of the lagoon, a small swamp (ca. 0.3 ha in area) connected to the southern end of the lagoon (Fig. 2), and four ephemeral ponds that formed 100-500 m from the swamp. These ponds developed in swales between sand dunes and typically filled between February and April.

Habitat

The swamp at the southern end of the lagoon was oval in shape and contained *Typha orientalis* to a width of 5 m, for approximately half its perimeter. About one third of

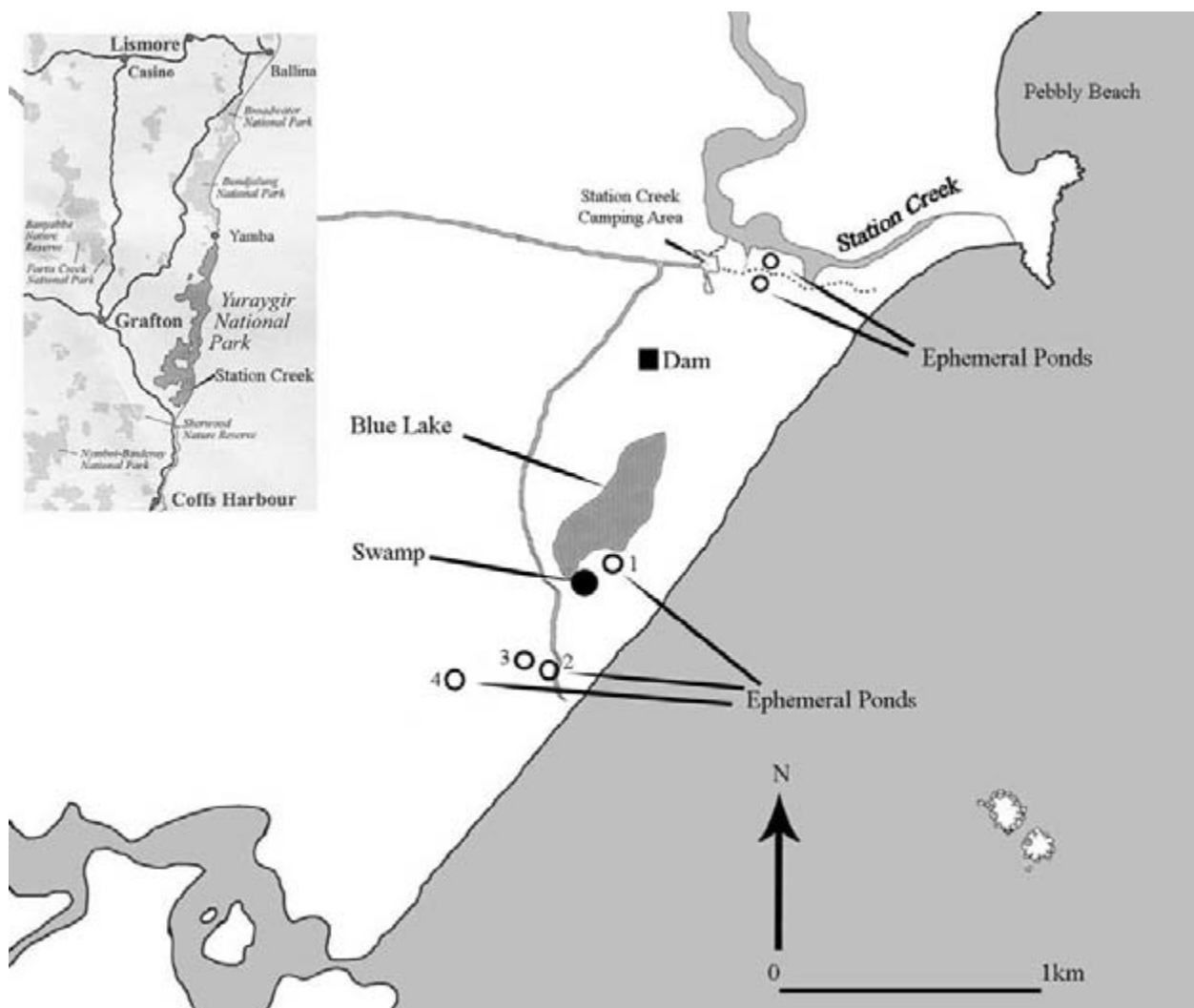


Figure 1. Locations of survey sites in Yuraygir National Park. Ephemeral ponds located south of Blue Lake are numbered 1-4.



Figure 2. The swamp at the southern end of the Blue Lake that was searched during each survey.

the inner part of the swamp contained a mix of *Eleocharis acuta*, *Eleocharis equisetina* and *Juncus polyanthemus*. There were scattered clumps of *Gahnia clarkei* along one broad edge. Some sub-aquatic vegetation was also present. The ephemeral pond areas were dominated by *Hydrocotyle bonariensis*.

The lagoon was surrounded on its long western and southern sides by paperbarks *Melaleuca quinquinervia*. On its eastern side it was lined by swamp oaks *Casuarina glauca*. On the water's edge, it was lined by *T. orientalis* and *G. clarkei* to a width of 2-20 m. *Gahnia clarkei*

dominated for about 150 m along the south-east corner. The vegetation in the lake was dominated by *Utricularia australis*, *Nitella* sp., *Najas* sp. and *Nymphaea capensis*. All but the latter were present on a seasonal basis (spring/summer). These ephemeral plants provided a dense cover from which male bell frogs called during spring.

Frog surveys

Surveys were conducted between August 1998 and March 2004. This period coincided with extreme variation in rainfall (Fig. 3). A severe drought occurred

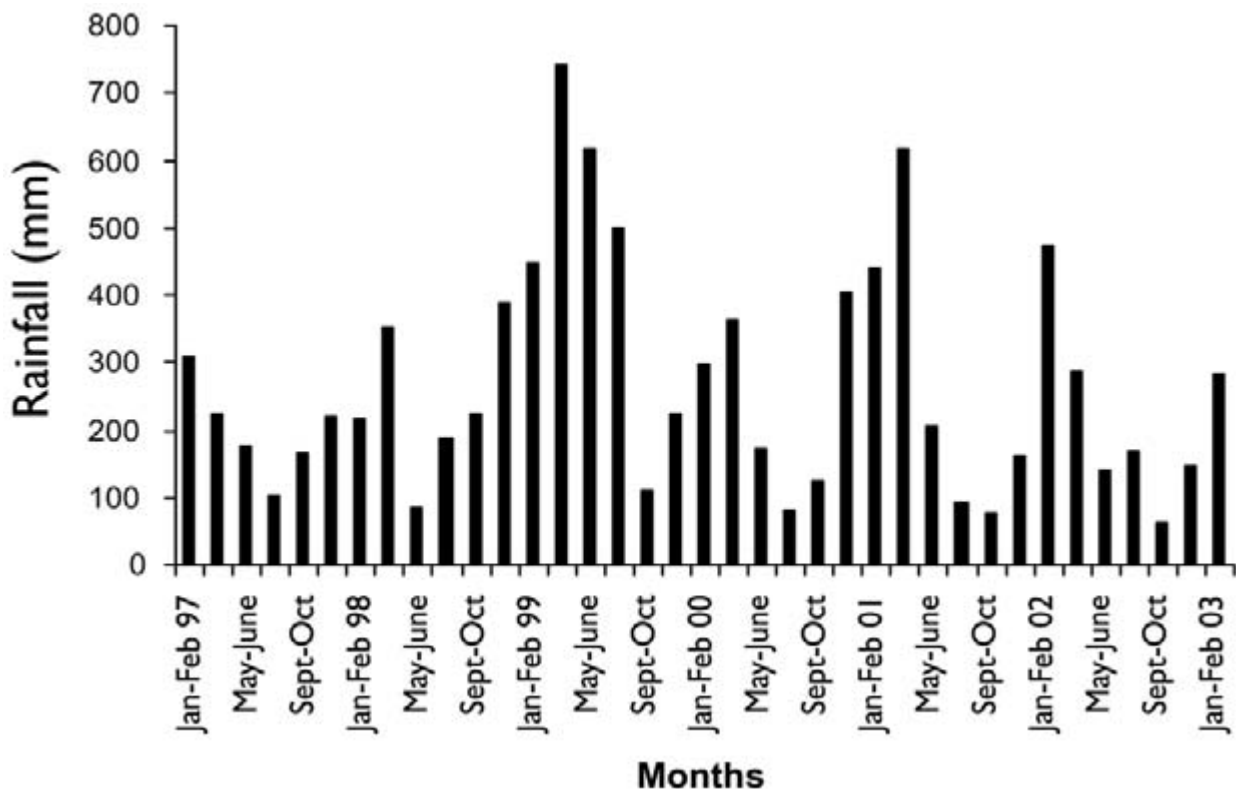


Figure 3. Rainfall pattern for Coffs Harbour between January 1997 and March 2003. Bars show the total rainfall for each 2-month period.

in 2002-3 (Fig. 4). In 1998/99, surveys were conducted each month, largely independent of rainfall events, in an attempt to maximise the number of frogs encountered and to gain an understanding of when breeding and metamorphosis occurred. In other years, surveys were conducted in October-November when males could be found calling spontaneously irrespective of any rainfall, and opportunistically in January-March following rainfall events so that breeding and ephemeral pond persistence could be monitored. Several day visits were also conducted in February-April to monitor pond persistence. Areas containing emergent aquatic vegetation were searched on foot with a 50 W spotlight during nocturnal surveys. At about every 20-30 m, the light was turned off and the bell frog call mimicked repeatedly for about 1-2 min. This was conducted around the southern perimeter of the lagoon, covering about 200 m each side (ca. one-third of the lagoon), through the swamp and through the locations of the ephemeral ponds. We followed the NSW frog hygiene protocol (NPWS 2000).

Bell frogs were captured and placed in plastic bags. They were sexed based on the presence of dark nuptial pads (unless recorded by call before capture), their snout-urostyle (SU) length was measured and most frogs were weighed. Notes were taken of the dorsal markings of each frog (excluding head), describing the relative coverage and locations of brown and green markings. Based on this they were placed into one of four categories: uniform brown; brown background with minor amounts of green dots and blotches; brown background with major amounts of green blotches; and uniform green. Frogs were scanned with a microchip reader to detect a uniquely-coded PIT tag. If none was present one was injected subcutaneously into the left side of each frog using a method similar to Christy (1996). The tag was manipulated through the skin to position it near the groin and away from the site of

insertion. This site was sealed with vetbond. The frog was later released near the point of capture. Frogs captured in 2004 were scanned but not tagged.

A fish scoop net was carried during most frog surveys so that sweeps for tadpoles could be conducted. This was to ascertain whether any were present but not readily seen and to capture tadpoles for species identification. Small numbers of tadpoles were collected and reared to metamorph stage to confirm species identity.

The SU lengths of male frogs captured in different months in 1998/99 were compared to assess growth rates across the period when they were active. Samples were pooled into early (August/September), mid (November) and late (February) season samples.

The Peterson method (Krebs 1989) was used to estimate the size of the bell frog population, based on the number of frogs marked in one period and the proportion of these detected in a second period. This could only be done using the male capture data for November 1998 and February 1999. The most important assumptions of this method are that the population is closed during the interval used and that animals have an equal chance of being captured (Krebs 1989). The first assumption is likely to have been true but the second may not be true. Therefore, any estimate should be treated with caution.

Results

Frog survey 1998-99

Ten nights were spent catching and tagging frogs between 28 August 1998 and 16 March 1999 (Table 1). Approximately 2-4 h per night were spent conducting these surveys. Seven male frogs were captured in late winter at the beginning of the active season. The greatest number was captured over 2-night periods in November



Figure 4. The dry conditions that prevailed during 2003 led to a severely reduced water level in Blue Lake in January 2004.

Table 1. Number of adult frogs captured at sites near Station Creek. Only dates when adult frogs were captured are shown. Female and male values are untagged frogs. Recaptures are frogs previously tagged. The single female recapture is shown in brackets. Estimates are given of the number of males calling.

Date	Females	Males	Recaptures	Calling Male Estimate
1998-99				
28-29 Aug	0	7	0	
20 Sept	2	8	0	
2 Nov	0	12	1	25
9 Nov	0	10	11	
22 Dec	2	6	6 (1)	
2 Jan	2	1	9	
4 Feb	1	11	8	
11 Feb	0	11	5	
16 Mar	0	1	0	
subtotal	7	67		
2000				
5 Oct	0	3	1	
11 Oct	1	9	2	
1 Nov	0	9	5	30
subtotal	1	21		
2001				
15 Nov	4	16	0	75
21 Nov	1	4	0	
25 Nov	0	0	1	
subtotal	5	20		
2003				
7 Mar	0	12	1	20
12 Mar	1	0	0	
2004				
14 Feb	3	9	0	
22 Mar	1	0	0	
Total	18	129		

and February, when over 20 adult males were tagged in each period. A single adult male was located and captured in March when metamorphs were emerging from breeding ponds (see below). No frogs were detected on a single night of survey conducted in late 1999.

Frog captures in November 1998 occurred in the small swamp at the southern end of Blue Lake; spontaneous calling indicated that at least 25 males were present (Table 1). This number was higher than the number captured on this night. Bell frogs were again captured in this swamp in late December and early January. In February 1999, the swamp site was so flooded (water depth >1.5 m) that a canoe was required to search it, but no frogs were detected. Subsequently, bell frogs were detected in four separate ephemeral ponds (each >0.2 ha, 20-80 cm deep) that had developed in the dune swales. Three were recaptured in a pond located 100 m north-east of the swamp (pond 1), two were recaptured in a pond located 300 m south of the swamp (pond 2) (Fig. 5), and four were recaptured in a pond 500 m south of the swamp (pond 4). Two were detected in the fourth pond located about 400 m south of

the swamp (pond 3) but could not be captured. Bell frogs were not detected in Blue Lake during this period.

The tagging of frogs over the course of the bell frog active season (August-March) revealed that at least 67 males and seven females were present at Blue Lake and its surrounds (Table 1). Thus, more adult male frogs were present than indicated by a single night's calling survey. Capture information for female bell frogs was scant (Table 1).

The Peterson estimate of the size of the male population was 116 bell frogs (95% confidence interval, 67 to 414). Given that 67 males were tagged over 10 nights, and almost 70% of 16 frogs captured on 11 February 1999 at the end of the survey period were untagged, it appears that the number of male frogs greatly exceeded the lower estimate. Recapture of tagged frogs during this season was quite high; 30 (64%) of 47 frogs that were tagged between August and December were recaptured in January and/or February. Of the frogs captured between August and February, 45% were captured more than once and four were captured on four different nights (Fig. 6). Of those captured once, 15% were captured on the last night in February when many frogs were active.



Figure 5. Ephemeral pond 2 located 300 m south of the swamp. The 4WD track is now closed.

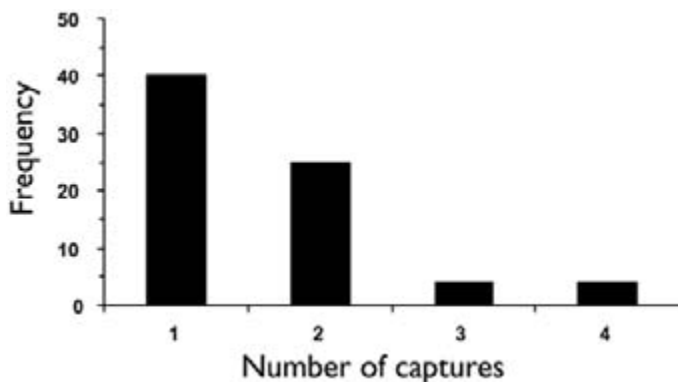


Figure 6. Frequency of the number of times an individual frog was captured.

Frog survey 2000-01

Twenty-one male and one female bell frogs were captured during three nights spent at Blue Lake in October and November 2000 (Table 1). One male frog captured during each of the three nights was first captured in November 1998, 300 m away in the swamp. This individual had grown 6 mm in SU length during this 2-year period. All other recaptures were from those marked during this period. Frogs were calling from the floating vegetation in the lake and from amongst the *Typha* on the lake's edge.

A count was conducted in November of calling males around the lagoon, which suggested at least 30 adult males were present. No frogs were detected in the swamp at the southern end of the lagoon and no ephemeral ponds were present surrounding the lagoon. No frogs were detected in early 2001.

Frog survey 2001-02

Twenty male and five female bell frogs were captured during two nights spent at Blue Lake in November 2001 (Table 1). No recaptures of tagged frogs occurred on either night. The four female bell frogs captured on 15 November was the highest number of females captured on any single night during the whole survey (Table 1). One male tagged on 21 November was the only frog captured on 25 November.

On 15 November, frogs were calling from the floating vegetation in the lake and from amongst the *Typha* on the lake's edge. Due to the strong spontaneous calling, it was possible to traverse one third of the lagoon and conduct a survey of calling males. Traverses of other parts of the lagoon suggested that this count was typical of the other two-thirds of the lagoon. Thus, it was estimated that at least 75 calling males were present on this night (Table 1). Again, no frogs were detected in the swamp at the southern end of the lagoon and no ephemeral ponds were present surrounding the lagoon. No frogs were detected in early 2002.

Frog survey 2002-3

No bell frogs were found during a survey conducted on 7 November 2002 during a severe drought, when the water level in Blue Lake was quite low. The swamp at the southern end was completely dry. No frogs were detected during several nights in early January 2003 when conditions were still exceptionally dry.

In late February 2003, extensive rain fell in north-east NSW. A survey was conducted on 7 March. A few frogs were heard calling at the southern end of the lagoon and

two were captured. A total of 15 males was heard calling in the swamp and 13 were captured (Table 1). One was a tagged frog that was first captured in the lagoon on 15 November 2001. This individual had grown 4 mm in length. Bell frog tadpoles (1-2 weeks old) were present in the swamp and the lagoon. The ephemeral pond 300 m south of the swamp was the only pond containing water. Further heavy rain fell on several days after this survey and the area was surveyed again on 12 March. All four ephemeral ponds contained water and all had an abundance of at least five species of frog attempting to breed, but no bell frogs were present. A single female bell frog was captured in the lagoon swamp. There was no male bell frog activity around this swamp or in the southern part of the lagoon.

Frog survey 2003-04

No surveys were conducted in late 2003. The site was visited on 14 February 2004 and 12 adult frogs, including three females, were captured in *Gahnia* on the eastern side of the lagoon. Male frogs were calling spontaneously. No adult frogs were detected in the swamp although metamorphs of several species were present.

Morphology

Of 94 adult frogs scored for dorsal colouration over a 2-year period, 27% were uniform brown, 54% were brown with minor green markings (Fig. 7), 18% were brown with major green markings and 1% were uniform green. Male frogs averaged $62.4 \text{ mm} \pm 0.4 \text{ s.e.}$ ($n=84$, range 56-72 mm) in SU length and weighed $15.6 \pm 0.6 \text{ g}$ ($n=33$). Females averaged $72.9 \text{ mm} \pm 1.8$ ($n=12$, range 65-83 mm) in length and weighed $29.2 \pm 2.2 \text{ g}$ ($n=10$).

There was no significant difference in lengths ($F_{2,55}=1.24$, $P=0.30$) for male frogs across the season: early ($63.7 \pm 0.8 \text{ s.e. mm}$, range 59-70), mid ($64.7 \pm 0.5 \text{ mm}$, range 59-71) and late ($63.2 \pm 0.8 \text{ mm}$, range 57-72). There was no significant difference (paired $t=1.10$, $df=13$, $P=0.29$) in length when comparing individual frogs captured at least seven weeks apart (mean interval 10.2 weeks) during this period. They initially averaged $63.8 \pm 0.7 \text{ mm}$ and later averaged $64.3 \pm 0.7 \text{ mm}$ in length.



Figure 7. An adult frog captured at Station Creek.

Breeding

There were 31 survey nights conducted in which to detect bell frog breeding stages at Station Creek (Table 2). Surveys were spaced through the active season in order to increase the likelihood that evidence of breeding would be recorded. Calling males were detected in the lagoon, in the adjoining swamp, and in four ephemeral ponds within 100-500 m of the swamp. Tagging revealed that frogs move among these sites. The pattern we observed over 5 years was that a moderate number of calling males (>20) was present in the lagoon in October and November when the adjoining swamp was dry or the water level low. Males called while floating on dense subaquatic vegetation in the lagoon. Small numbers of tadpoles were detected in the lagoon on several occasions, but no bell frog metamorphs or subadults ($SU < 50 \text{ cm}$) were subsequently observed.

When the water level in the swamp was approximately 20-50 cm deep, and the water level high in the lagoon, calling males (>10) were detected in the swamp but not in the lagoon. This was observed each month from August to March, except when the swamp was dry (October), or when water levels were very high (ca. 2 m deep) and ephemeral ponds were present (February). Tadpoles were seen in this swamp on a number of occasions, including many hundreds in November 2000 and March 2003. Net surveys were conducted in association with adult surveys, but few if any bell frog tadpoles were detected at other times (Table 2). Single subadults were observed in January and October 1999. Eight metamorphs were observed in April 2003. In February 2004, a single metamorph was detected while 5 weeks later three metamorphs were observed (Fig. 8). On these two survey nights numerous metamorphs of *L. nasuta*, *L. dentata*, *L. gracilentia* and *L. fallax* were seen.

Bell frogs were first observed using the ephemeral ponds surrounding Blue Lake on 4 February 1999. Calling males were located in each of the four ponds. An amplexing pair was found in pond 1, and an egg mass was discovered the next day. Some bell frog tadpoles were already present. On 16 March 1999, 64 metamorphs were recorded around this pond. On 25 March, about 15 metamorphs were recorded in this area but the water had almost drained away. It is presumed that over 100 metamorphs were produced from this pond. None were seen at the other three ponds in the area.



Figure 8. Metamorphing frog detected in the swamp in March 2004. Most metamorphs were predominantly brown.

Table 2. Breeding events recorded at sites near Station Creek. Survey nights involved searches of the lagoon (L), swamp (S) and ephemeral pond (EP) areas. Values are the number of each life stage at a given site. For tadpoles, only sites where >100 were seen are given. - = none detected.

Year/Period	No. survey nights	Tadpoles	Metamorphs	Subadults
1998				
Jan – Apr	2	-	-	-
Aug - Dec	7	-	-	-
1999				
Jan – Apr	4	EP: 1000s	EP: 64	S, EP: 2
Aug - Dec	1	-	-	S: 1
2000				
Jan – Apr	0			
Aug - Dec	4	S: 100s	-	-
2001				
Jan – Apr	2	EP: 100s	-	-
Aug - Dec	3	-	-	-
2002				
Jan – Apr	1	-	-	-
Aug - Dec	1	-	-	-
2003				
Jan – Apr	4	L, S: 100s	S: 8	-
2004				
Jan – Apr	2	-	S: 4	-

All ponds filled in other years, but did not retain water for as long as in 1999, or they contained water later in the year when frogs could not breed. In mid-April 2001, ponds 2 and 4 had abundant water and hundreds of tadpoles, but none were identified as *L. aurea*. Metamorphs of *L. fallax*, *L. dentata*, *L. caerulea* and *L. gracilentia* but not *L. aurea* were observed around pond 2. On 12 March 2003, ponds 1, 2, and 4 had water, but none contained bell frog tadpoles. Pond 3 was dry. On 10 April 2003, pond 1 had dried, pond 2 had a 5 cm depth of water and pond 4 had a 10 cm depth of water. Metamorphs of *L. nasuta*, *L. caerulea*, *L. fallax*, *L. dentata*, and *L. gracilentia* were observed.

Another two ephemeral ponds occurred 200 m directly east of the Station Creek camping area. These were more prone to drying than the ponds south of the lagoon. The pond that retained water the longest in this area was reduced to a 1 m diameter depression on 23 February 2001 and again on 15 April 2001, representing successive filling and drying events. Several bell frog tadpoles were present in this depression in February, but it would have completely dried out before they completed metamorphosis. A single bell frog tadpole was detected among other tadpoles in April, but it would not have survived before the pond dried out again. The pond filled in early March 2003 but no bell frog tadpoles were present. In March 2004, it was again reduced to a 1 m diameter depression 10 cm deep but contained no tadpoles. No bell frog metamorphs or subadults were detected around these ephemeral ponds despite many nights of survey (Table 2). A single subadult was detected in the *Typha* at the footbridge, 100 m west of one of these ponds on 7 October 1999.

Discussion

Population Size and Dynamics

This study recorded over 70 adult bell frogs in two different years at Station Creek. One count was based on the total number of individuals tagged over a 5-month period; the second count was based on a survey of calling males extrapolated for the whole of the lagoon. Based on mark-recapture, it was estimated that the bell frog population in 1998-99 numbered more than 100 adult males.

Earlier surveys at Station Creek observed 10 or less adults, suggesting a very small population (Clancy 1996; Lewis and Goldingay 1999). Differences in numbers detected may be due to surveys coinciding with dry conditions, or because they followed a period of intense breeding activity when use of breeding sites was reduced. It is unlikely that there had been a dramatic increase in the size of the population. For example, on several occasions few frogs were detected 1-2 weeks after a night of high frog activity (see also van de Mortel and Goldingay 1998).

The small number of females relative to males captured during this study is indicative of either a sampling artefact or an extremely biased sex ratio in the population. Males can be readily located and counted when calling. Surveys did not always rely on calls for detecting frogs and many males were captured during periods when calling did not occur. However, surveys were focused on the vegetation in the wetland habitats where males may spend more time. Amplecting pairs are quite obvious when conducting surveys but relatively few were seen. It is likely that females may show markedly different patterns of habitat use compared to males.

The continued capture of untagged males during the 1998/99 season suggested that there was a continued mixing of male frogs. All 47 frogs captured between August and December 1998 were within the 0.3 ha swamp. This site was easy to search and it appeared that a large proportion (>50%) of active frogs were captured on a given night. Nine of these frogs were recaptured more than one month later in ephemeral ponds 300–500 m from the swamp, demonstrating the mobility of these frogs. The recapture rate in 1998/99 was high, with 30 of the 47 frogs (64%) tagged between August and December recaptured in January or February. This also suggests that on-going detectability following tagging was high and that the majority of tagged frogs didn't move far from a home site.

An important question that arises from the 1998–99 capture data is whether the continued influx of untagged male frogs was due to new individuals simply being detected for the first time or whether subadults were reaching adult size at different times during the season. If the latter, then it would be predicted that some months should be dominated by smaller size classes. However, there was no difference in mean length among frogs measured early, mid or late in the active season. Furthermore, individuals that were measured 10 weeks apart grew by only 0.5 mm, suggesting that growth within a season is slow. The presence of several individuals of 70 mm and < 60 mm length during each month suggests that several cohorts were present concurrently but it is not known whether this represents individuals that metamorphosed early and late in the season, or those from different years.

Due to the lack of difference in frog sizes at different times of the season and the low growth rates during the season, it appears that male adult size is attained before the onset of the breeding season (e.g. in August). This suggests that limited recruitment to the adult male population occurred during the season. Gravid females were detected from mid-October through to early March. Therefore, there was potential for individuals of differing length if metamorphs emerged at different times of the year. It is also likely that some variation in SU length was a consequence of differential growth rates among individuals.

Williamson and Bull (1996) found that most growth in the eastern froglet *Crinia signifera* occurred within 12 months of metamorphosis and that most reached sexual maturity in their second year (i.e. 18 months after metamorphosis). Most subadult frogs were collected in months outside the breeding period. Such observations were not made for the bell frog at Station Creek, suggesting that subadult male frogs matured rapidly in the months before the onset of the breeding season, or that subadult male frogs occupied different habitats away from the breeding sites. Due to the dense and extensive vegetation that surrounded the breeding sites, a search of these areas was not undertaken. This could be investigated by marking metamorphs and determining whether many are able to reach maturity before the next breeding season.

Only 2 of 134 individuals tagged during this study were recaptured outside the season in which they were first tagged. The lack of recaptures across years compared to within years suggests that most adult male frogs survive

for only about two years. Only one female was ever recaptured, occurring 3 months after tagging. A detailed radio-tracking study may provide some insight into what happens to individuals after the breeding season.

Breeding

Breeding success appeared to be uneven across years. Only three observations were made of metamorphs emerging from a breeding site across the 6-year period of the study. Over 100 metamorphs were produced in mid-March 1999 from a single ephemeral pond but no other site. Eight metamorphs were observed in the swamp in mid-April 2003 and another four in March 2004 but none at any other site, suggesting a low breeding success in these years. Christy (2001) recorded considerable interannual variation in spawning activity by bell frogs in Sydney. This suggests that some variation in the number of metamorphs may arise from variation in the number of spawns deposited.

Surveys were conducted at Station Ck in most years in February and November but no metamorphs were observed around the lagoon or the swamp, despite tadpoles being observed on several occasions. It is likely that some metamorphs escaped detection. However, van de Mortel and Goldingay (1998) observed juvenile frogs around the periphery of Coomaditchy Lagoon, Port Kembla, over a 5-week period following a major breeding event. Furthermore, Goldingay and Lewis (1999) regularly observed juvenile frogs during bimonthly surveys of breeding habitats at several sites at Port Kembla. These observations suggest that surveys at Station Ck should have detected juveniles much more frequently than was the case, if breeding had been more successful than what is inferred.

Large numbers of tadpoles were seen in the ephemeral ponds over several years, indicating the readiness of bell frogs to use these breeding sites. However, repeated observations between 2001 and 2004 revealed that these ponds were unreliable breeding sites because they often did not retain water for a sufficient period (5–6 weeks) for metamorphosis to occur or they filled too late in the breeding season to be useful. Ephemeral ponds may not reliably persist for a 6-week period because the hydrology of the area has been altered by past sand-mining (see Clancy 1996). Richter *et al.* (2003) found that extreme annual variation in reproductive success in the endangered dusky gopher frog *Rana sevosia* was mediated by variation in pond persistence.

The successful development of bell frog tadpoles in one ephemeral pond between February and March 1999 offers an insight into levels of rainfall required for these ponds to persist in the area. In 1999, rainfall exceeded 400 mm in January–February and 700 mm in March–April (Fig. 1). Only in 2001 was there a similar pattern between 1997 and 2003. However, observations in February and April 2001 revealed that the ephemeral ponds did not sustain water for a sufficient period for tadpoles to complete development. Whether this was a consequence of lower rainfall in the previous July–October or simply that rainfall in March–April was inadequate is unknown.

High spring rainfall was implicated in the breeding success of bell frogs at Port Kembla, where it appears a sufficient water level in the lagoon enables eggs and tadpoles a greater chance of escaping predation by *Gambusia holbrooki* (Goldingay and Lewis 1999).

Our observations suggest that the lagoon and the adjoining swamp at Station Ck were associated with poor breeding success, despite frogs apparently attempting to breed there in most years (amplecting pairs were observed at both sites). It is unlikely that pairs that commenced amplexus at those sites would have travelled far to spawn. Hundreds of bell frog tadpoles were observed in the swamp in March 2003, but in April only eight metamorphs and a single large tadpole were seen, despite an intensive search. The reason for the poor breeding success may be due to the presence of fish. The lagoon had up to seven species of native fish, while the swamp contained four of these species (empire gudgeon *Hypseleotris compressa*, firetail gudgeon *Hypseleotris galli*, pacific blue-eye *Pseudomugil signifer* and eel *Anguilla* sp.). Pyke and White (2000) found that native fish preyed on *L. aurea* tadpoles, although possibly with less intensity than the exotic *G. holbrooki*.

One of the benefits of our study is that it is the first in relatively undisturbed natural habitat to investigate aspects of the population ecology of the green and golden bell frog. Thus, these observations of poor breeding success in a natural permanent water body may offer an explanation for the very high fecundity in this species. Earlier authors have stated that the high reproductive output suggests that this frog is a colonising species and that it is likely to be associated with disturbed environments or newly created habitats (Pyke and White 2001; Pyke *et al.* 2002). However, selection could have favoured high fecundity due to fish predation in natural habitat. Large egg masses allow some escape from predation and greater exploitation of reproduction in ephemeral ponds than in permanent waterbodies. Christy (2001) suggests that it may provide a bet-hedging strategy if females can regulate the number of eggs in a clutch and have multiple clutches in a season. They would then be able to deposit in different pond environments during a breeding season.

Conservation and Management of Bell Frogs in Northern NSW

Several key observations were made during this study that have important implications for the conservation of the green and golden bell frog in northern NSW. Firstly, frogs in this population are morphologically distinct from southern populations. Secondly, the population is much larger than previously suggested. Thirdly, breeding is erratic and should be the focus of management attention.

A major focus of conservation strategies should be to conserve populations throughout the geographic range of a species. This should be a priority from the viewpoint of retaining existing genetic diversity and local adaptation, as well as minimising exposure to correlated adverse environmental conditions. Such an approach should place a particular significance on populations at the edge of a species' range (e.g. Lesica and Allendorf 1995). From this perspective, the population at Station Ck is one of great significance for the green and golden bell frog because it is the largest at the northern end of the range. Moreover, the population was dominated (81%) by predominantly brown-coloured individuals (see also photo in Clancy 1996). This is quite different to bell frogs studied at Port Kembla where the population was dominated by green individuals (unpublished data). These morphological differences may suggest that some visible genetic differences exist between parts of the geographic range. Further investigation of this phenomenon is required.

The bell frog population at Station Ck contains at least 100 adult males. If the sex ratio is closer than observed to 1:1, then the total population size may be as high as 200 adult frogs. Greer and Byrne (1995) recorded an even sex ratio in *L. aurea* metamorphs in Sydney, while Williamson and Bull (1996) observed an even sex ratio in *C. signifera*. However, if the number of adult females is indeed low, this will limit the overall size of the population and its capacity to expand. Whatever the case, management focussed on improving breeding success (see below) should aim to enhance female numbers.

Observations conducted over more than five years during this study suggest that breeding success at Station Ck is highly variable. The permanent waterbodies have abundant fish populations that appear to limit breeding success. On the other hand, ephemeral ponds have a limited ability in most years to retain water for a sufficient period (5-6 weeks) for metamorphosis to occur. Whether this is the result of historic degradation of the dunal habitat is unknown. These factors suggest that management should explore the use of experimental habitat restoration directed at the breeding habitat. There should also be some investigation of the value of fish enclosures in the lagoon or artificial breeding ponds surrounding the lagoon. The collection of spawn for captive or field rearing of tadpoles for subsequent release should also be considered.

The observations at Station Ck further highlight the importance of different types of breeding sites within close proximity (Goldingay and Lewis 1999). Hamer *et al.* (2002) also found that sites occupied by bell frogs were in close proximity. This is an important observation that should be used when developing management plans for the species.

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